Plant Responses and Adaptation to Drought

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Concept

Among these abiotic stresses, drought is the most complex and devastating on a global scale and its frequency is expected to increase as a consequence of climate change. Water shortage is expected to lead to global crop production losses of up to 30% by 2025, compared to current yields (The World Economic Forum 2009). Consequently, drought stress represents a major threat for sustaining food security under current conditions and will be more of a danger in the future, as climate change is projected to induce more frequent and more intense higher temperatures and drier conditions in many regions of the world.

The primary effect of drought stress is largely a reduction in plant growth, which depends on cell division, cell enlargement, and differentiation, and involves genetic, physiological, ecological and morphological events and their complex interactions. These events are seriously inhibited by drought stress, which adversely affects a variety of vital physiological and biochemical processes in plants. Disruption of these key functions limits growth and developmental processes and leads to reductions in final crop yield (Fig. 1).

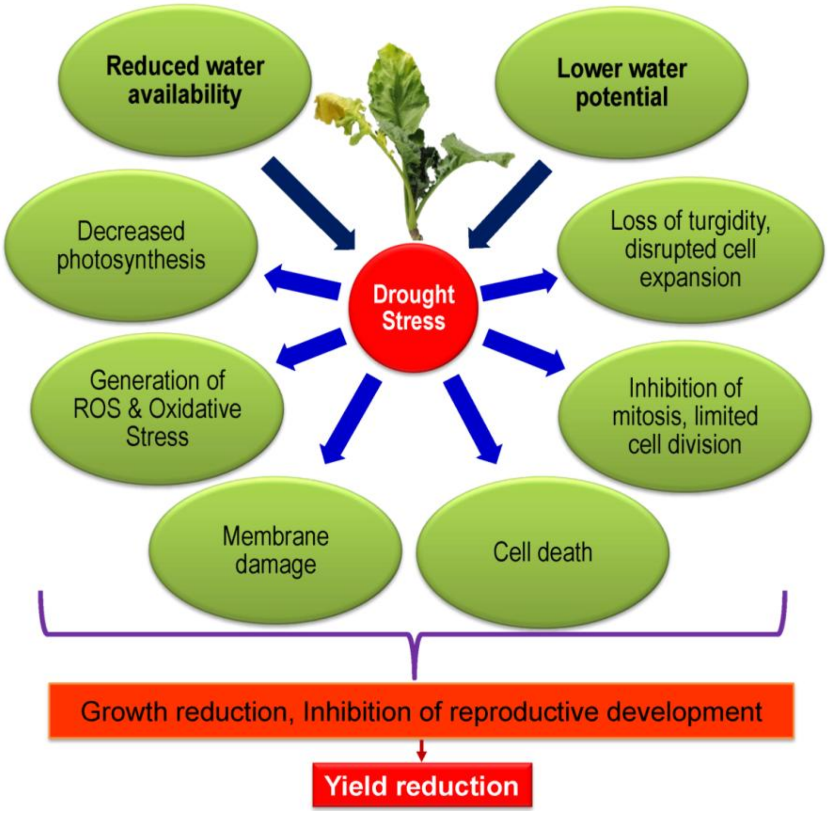


Fig. 1 Possible effects of drought stress in plants. Reduced water uptake results in a decrease in tissue water contents and reduction in turgidity due to drought. Under drought stress conditions, cell elongation in higher plants is inhibited by reduced turgor pressure. Drought stress also impair mitosis, cell elongation and expansion, which result in growth reduction. Severe drought conditions limit photosynthesis due to a decrease in the enzymes' activities required for photosynthesis. Drought stress disturbs the balance between the production of reactive oxygen species and the antioxidant defense, causing oxidative stress. Final consequence of the drought stress is the reduction of yield.

Effect of drought on crop plants

Germination

Drought is one of the major environmental factors, which determines the success or failure of plants establishment because to be germinated one of the prime requirement is the presence of water. Drought stress decreases germination and seedling growth which lead to the reduction of plant growth and yield.

Plant growth

Cell is the basic structural unit of all living organisms. For cell growth one of the most basic requirements is water that causes cell expansion which further resulted in cell growth though the cell division process is less affected as compared to cell expansion by drought. Thus reduced cell growth due to water scarcity affects the growth in whole plant level also (Fig. 2). Drought causes growth reduction in multiple ways. Drought inhibits cell expansion and reduces stomatal opening and carbohydrate supply, ultimately decrease growth. Moreover, drought can reduce decomposition process and thus nutrient availability.

Fig. 2 Drought stress-induced growth reduction (a) and wilting (b) in rice (*Oryza sativa*) and jute (*Corchorus capsularis*) plants

Plant water relations

Drought stress has great impact on plant water relations. The major attributes which are effected by drought are relative water content (RWC), leaf water potential, osmotic potential, pressure potential, and transpiration rate are the major attributes of plant water relations. The reduction of water potential is also greatly dependent on crop species, varieties and level of stress. This is due to differences of their tolerance to drought. For instance, drought-tolerant genotypes maintained higher leaf water potential for longer and wilted later than sensitive genotypes upon exposure to drought. Tissue water contents decreased linearly with increased severity of drought. Water use efficiency (WUE) also greatly affected by drought but this effect is dependent on the crop species and varieties.

Stomatal conductance and gas exchange

Stomatal closure is one of the earliest plant responses under drought concomitant with the reduced water potential and turgor associated with even a small decrease in relative water content. As studied by many researchers stomatal conductance is affected by drought. Drought sensitive and drought tolerant plant show different stomatal movement in response to water deficit condition. Stomatal conductance and carbon assimilation are maintained in drought sensitive crops after the water potential falls whereas in drought adapted plant stomata may be closed at dry and hot environment in presence of high tissue water content. Stomatal closure has a strong interaction with photosynthesis.

Over 95% of water loss from plants can occur by transpiration through the stomatal pores. Therefore, it is important for plants to be able to balance the amount of CO_2 being brought into the plant with the amount of water escaping as a result of the open stomatal pores. Stomata close progressively as drought progresses, followed by parallel decreases of net photosynthesis. As CO_2 availability in the chloroplasts depends on stomatal conductance, it has been frequently assumed that drought decreases photosynthesis simply by closing stomata and limiting CO_2 availability.

Photosynthesis

Drought affects photosynthesis in multidimensional ways. It has adverse effect photosynthetic apparatus and their membrane, enzymes, absorption processes. Upon imposition of drought one of the prime responses of plant is closing or little movement of stomata to reduce water loss by transpiration which is more prominent in the plant species of drought prone areas. Drought stress affects photosynthesis by reducing leaf area, enhancing stomatal closure, decreasing water status in the leaf tissues, reducing the rate of CO_2 assimilation, causing ultrastructural changes in chloroplasts, affecting electron transport and CO_2 assimilation reactions impairing ATP synthesis and ribulose bisphosphate (RuBP) generation, and altering the level of photosynthates in the tissues (Fig. 3). Water stress causes an imbalance in the hormone level in plants. Due to alteration in hormonal balance, concentrations of many key enzymes of photosynthesis decline in water-stressed plants (Fig. 3). Since drought stress causes decrease in relative water content and water potential of leaves progressively decrease stomatal conductance, leading to decline in CO_2 assimilation, and reduced rate of photosynthesis. Stomatal closure is among the earliest responses of plants subjected to water stress and it is generally assumed to be the main cause of drought-induced decrease in photosynthesis because stomatal closure leads to decrease in CO_2 intake by mesophyll cells and thereby decreased CO_2 assimilation and net photosynthesis.

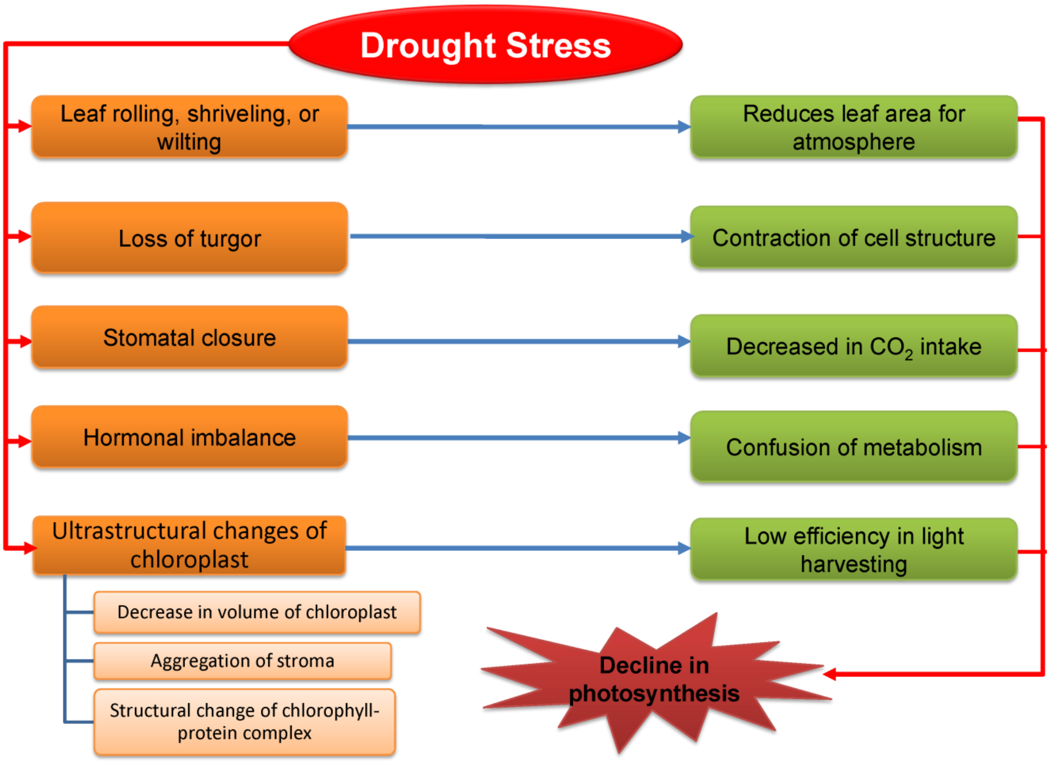


Fig. 3 Possible reasons for the decline in photosynthesis in plants under drought stress

Reproductive development and seed formation

Drought directly affects the reproduction process of plants. Early reproductive stages, micro- and megasporogensis are the most sensitive among the sub-phases. Pollen viability, germination, pollen tube growth, stigma viability and receptivity, anthesis, pollination, fertilization, and embryo

development are severely vulnerable to drought stress. Lacking of any of these processes causes embryo abortion that ultimately affects the yield. Decreased water potential in the floral tissues including pollen, female gametophyte and stigma decreased carbohydrate or nitrogen supply to the floral parts are common in drought stress. Drought stress after fertilization decreases seed size rather than seed number.

Yield attributes and yield

Drought stress both during vegetative and early reproductive growth reduces yield. The assimilate of vegetative parts contributes to yield and that is why vegetative stage drought is important and more emphasizely drought in reproductive stage diminishes the yield directly by hampering the reproductive parts or developmental stages which are very susceptible to all kinds of stress including the drought. Drought hampers the yield by obstructing the panicle, peduncle, rachis, tiller growth and development; reducing the number of seeds, seed size and seed quality. Reduction of final yield were measured in different crop plants under drought stress condition.

Drought and oxidative stress

Water deficit makes the cellular content more viscous for which the protein denatures, thus membrane of photosynthetic apparatus as well as cell membrane denatures. At the same time the enzymes of calvin cycle are inactivated, the efficiency of carboxylation reaction and CO_2 fixation by RuBisCO is reduced and results in increased photorespiration which is one of the major reason of ROS production.

Drought induced stomatal closure is another common phenomenon which reduces the CO_2 availability in the fixation site of calvin cycle. The rate of regeneration of $NADP^+$ is also reduced under drought, thus the electrons of ETC cannot be accepted properly, finally excess reduction of ETC causes leakage of electron to O_2, production of ROS ($O_2^{\bullet-}$, $^1O_2$, H_2O_2 and $OH^{\bullet}$).

Additionally, under stressful condition chloroplasts receive excessive excitation energy beyond their capacity to bind it and ferredoxin remains over reduced condition during photosynthetic electron transfer, the electrons having high state of energy are transferred from PSI to molecular oxygen.

In plant, the normal ROS steady-state level is disturbed by drought stress where initially the enhancement on ROS production due to stomatal closure shifts the equilibrium upwards and this triggers defense signal transduction pathways. But prolonged drought stress result in exacerbated ROS production that cannot be counterbalanced by the antioxidant system, leading to deleterious oxidative events which ultimately result in cell death (Fig. 4).

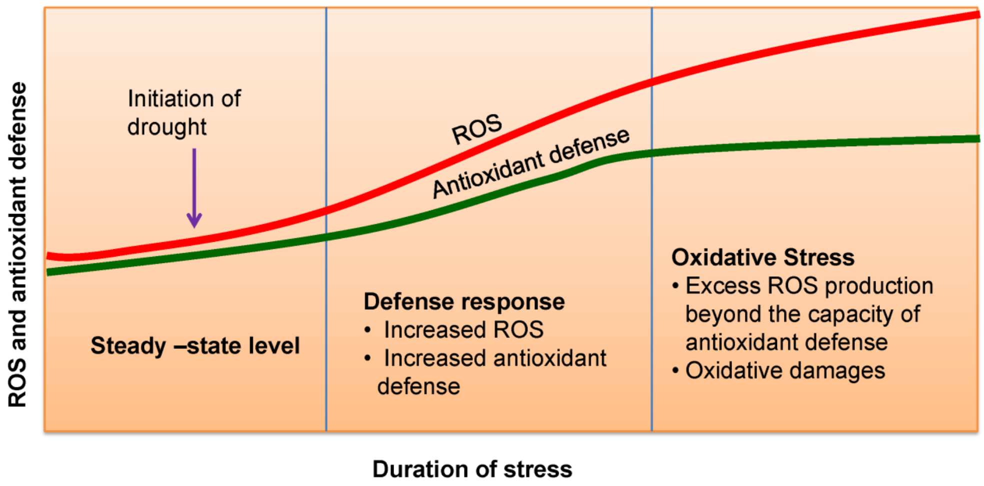


Fig. 4. Different phases of drought stress in terms of oxidative stress and antioxidant defense in plants

Plant adaptative responses to drought

Plants growing in drought stress may have the ability to control / avoid stress by escaping (enduring drought) or tolerating stress (by developing succulent or non-succulent habit). These two capabilities are collectively termed as Drought Tolerance.

1. Drought evading plants

These plants remain under dormant / perennation to avoid stress period by seeds and shoots. Such plants complete their life-cycle in few weeks within the rainy season (e.g. sorghum). They are called as ephemerals. These plants also prolong their life cycle for some time based on the necessity. They reduce water loss by certain mechanism.

2. Succulents

The CAM plants store enough water in their tissues. Their stomata open at night. They have thick leaves and possess modifications (such as phyllodes and phylloclades) under water stress conditions. They fix carbon during day time with the help of malic acid and CO2, which is released internally during respiration.

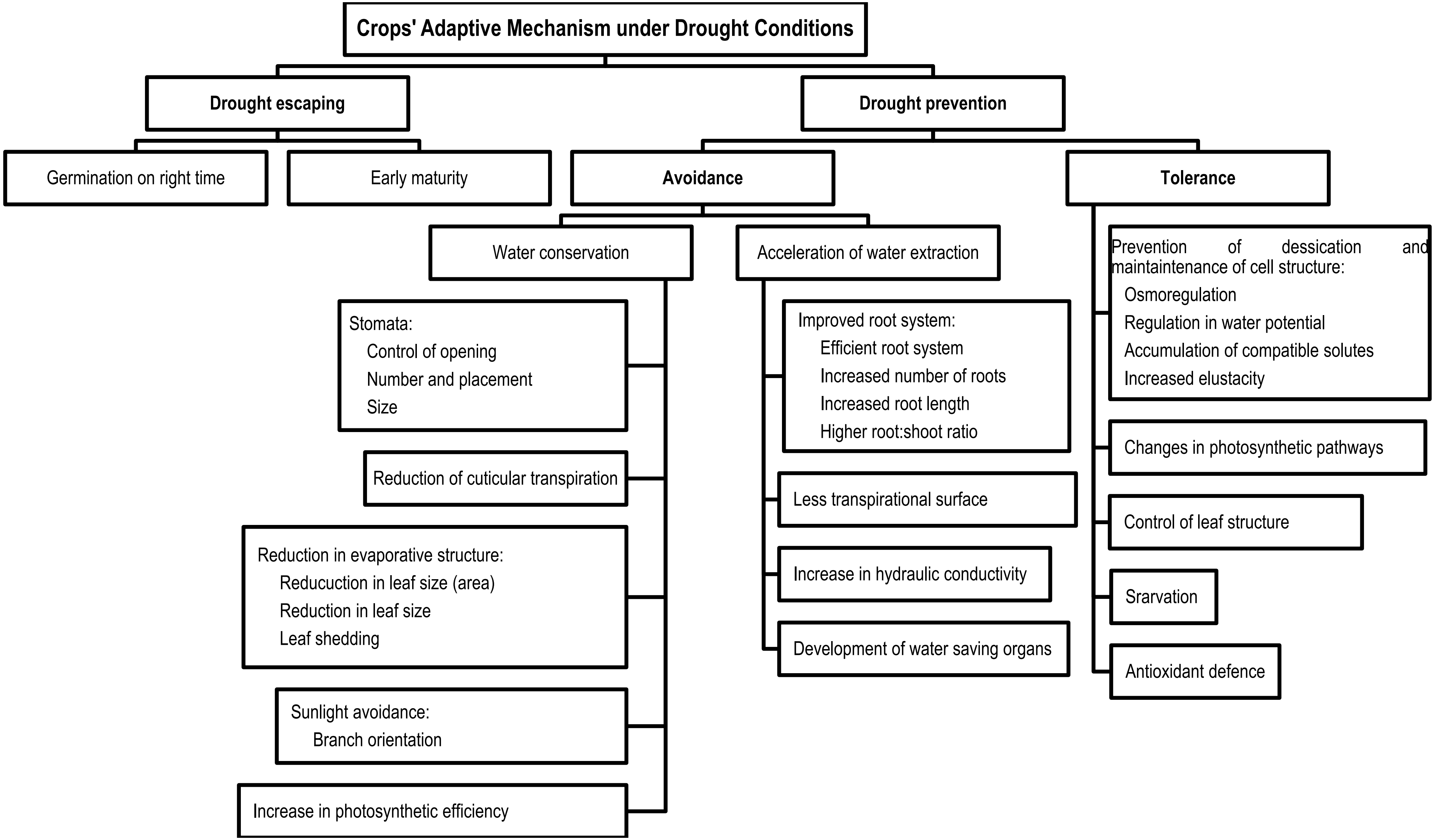
3. Non-succulents

These plants endure drought with the following adaptive features:
- Smaller leaves with thick cuticle
- Sunken stomata with hair (pubescence) eg. Nerium
- Shedding their leaves during summer to avoid excess water loss
- Dehydration of protoplasm
- Reducing enzyme activity
- Favouring the syntheses of ABA (stress hormone) and Ethylene (senescence hormone)
- Closing stomata due to increase ABA concentration, thereby reducing water loss

Thus, because of these special features, succulents and non-succulents grow well under drought conditions. They are not or least affected by stress. Similarly, the arid zone plants also develop mechanisms to tolerate water stress, hence they are not adversely affected in terms of growth and yield. But, the non-arid zone plants suffer heavy loss in growth and yield because they do not have above said mechanisms to tolerate the stress.

4. Drought Resistant Plants
These plants resist the water stress situations due to the following adaptive features / mechanisms. Therefore, these plants can be grown in drought facing / arid-zone areas.
- Higher rate of photosynthesis because of efficient carboxylating systems (increased activities of RuBPCase, PEPCase, Malic Enzyme etc.)
- Store much water for proper hydration of protoplasm
- Fix carbon by C4 pathway rather than usual C3
- Producing "Aquaporins" – an intrinsic membrane protein in water-stressed plants, which enhance the water flow by 10 – 20 folds (Chrispeels and Maurel, 1994).

Drought Resistance Mechanism
The ability of a crop species or variety to grow and yield satisfactorily in areas subjected to periodic water deficits is termed as drought resistance
Types of drought resistance
- **Drought escape**: The ability of a plant to complete the lifecycle before serious soil and plant water deficits develop.
- **Drought tolerance with high tissue water potential**: The ability of the plant to endure periods of drought whilst maintaining a high plant water stress. This is also referred to as **drought avoidance** (Levitt, 1972).
- **Drought tolerance with low tissue water potential:** The ability of the plant to endure periods without significant rainfall and to endure low tissue water potential.



Crops' Adaptive Mechanism under Drought Conditions
Drought escaping
Drought prevention
Germination on right time
Early maturity
Avoidance
Tolerance
Water conservation
Acceleration of water extraction
Stomata:
Control of opening
Number and placement
Size
Reduction of cuticular transpiration
Reduction in evaporative structure:
Reducuction in leaf size (area)
Reduction in leaf size
Leaf shedding
Sunlight avoidance:
Branch orientation
Increase in photosynthetic efficiency
Improved root system:
Efficient root system
Increased number of roots
Increased root length
Higher root:shoot ratio
Less transpirational surface
Increase in hydraulic conductivity
Development of water saving organs
Prevention of dessication and maintaintenance of cell structure:
Osmoregulation
Regulation in water potential
Accumulation of compatible solutes
Increased elustacity
Changes in photosynthetic pathways
Control of leaf structure
Srarvation
Antioxidant defence

Soil and plant microclimate management for plant drought tolerance

Drought stress includes different agronomic, soil, and climatic factors which vary in the time of occurrence, duration, and intensity (Fig. 5). It has effect on yield and can also diminish benefits of crop handling performances including management of fertilizer or pest and disease. Drought management strategies are very important and have to concentrate on extraction of available soil moisture, crop establishment, growth, biomass, and grain yield. There are many agronomical ways to manage drought stress such as control of field irrigation methods (surface or furrow, sprinkled, and drip) and identification of drought resistance sources through developing screening methods under environmental conditions.

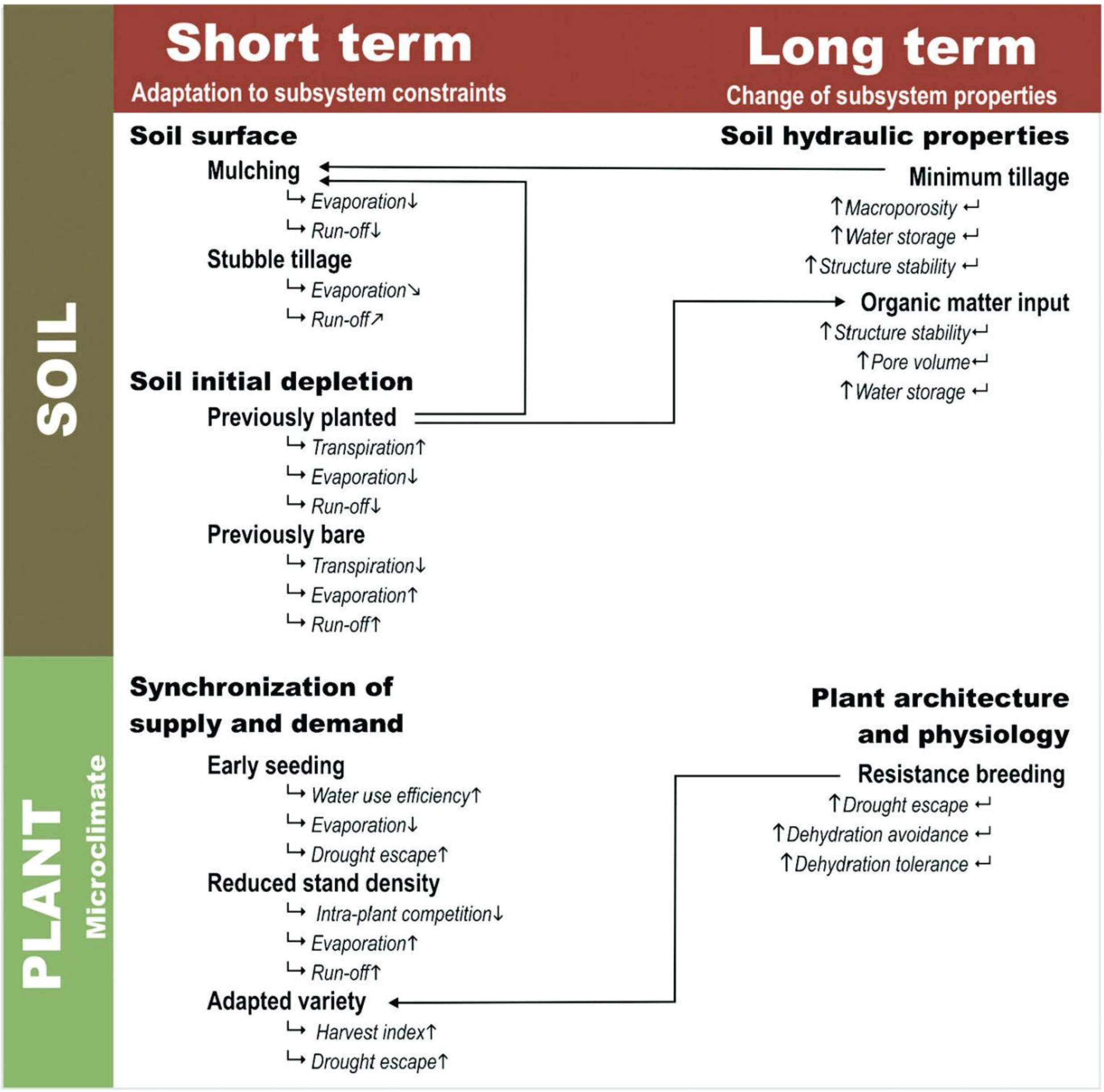


Fig. 5: Short- and long-term management measures and their effects on water-use efficiency and drought stress resistance. Short-term measures adapt the cropping system to site conditions, while long-term measure strive to improve environmental constraints of a site. Arrows indicate concomitant and/or successive effects of a given practice on other measures (Bodner et al. 2015).

Mulching in drought stress mitigation

In rainfed areas, judicious use of water is essential for increasing area under crop production. One of the promising agro techniques under this situation is the use of various moisture conservation measures. Mulching has been advocated as an effective means of soil moisture conservation as it acts as an insulating barrier, which helps to check evaporation from the soil surface.

Mulching is an agricultural technique in which the use of organic materials (plant residues-straw, hay, groundnut hulls, leaf and compost, peat, wood products-saw dust and animal manures), and synthetic materials (paper, polyethylene, wax coated papers, aluminium, steel foils and asphalt spray emulsions etc.) are involved for the purpose of increasing soil productivity. This technique modifies soil and air microclimate through temperature moderation, and protects the roots of plants from heat, cold or drought.

Antitranspirants for water stress mitigation

Antitranspirants are chemicals capable of reducing the transpiration rate in plants when applied to plant foliage. Kaolin is a non abrasive, non toxic aluminosilicate clay mineral that is formulated as a wettable powder. Reflecting type antitranspitants were non toxic and effective for a longer period than stomatal closing types. Kaolin spray decreased leaf temperature by increasing leaf reflectance and reducing transpiration in many plant species at high solar radiation levels. Limewater is the common name for a diluted solution of calcium hydroxide which also acts as a reflecting agent when applied on leaves. Atrazine is basically a herbicide, which in lower concentration act as an antitranspirant by inducing stomata closure. Atrazine as antitranspirant reduces the crop growth, affect the closure and opening of leaf stomata, also forms thin layer on leaf surface.

Leaf temperature of rapeseed, treated with kaolin was lower than ambient air temperature which resulted in higher relative leaf water content (Patil and De, 1978). Tomato plants treated with kaolin resulted in 53 per cent reduction in stomatal conductance and thereby 21 per cent increase in marketable yield (Cantore *et al*. 2009).

Nutrient management for water stress mitigation

The detrimental effects of drought can be minimized by adequate and balanced supply of mineral nutrients. Mineral-nutrient status of plants plays a critical role in increasing plant resistance to drought stress. Macronutrients like nitrogen, potassium and calcium can reduce the toxicity of ROS by increasing the concentration of antioxidant enzymes in the plant cells, which help in mitigating water stress. Similarly, nutrients like phosphorus, potassium, magnesium and zinc improve the root growth, which in turn increases water uptake and helps in stomatal regulation thereby enhancing drought tolerance. Sulfur enhances drought stress tolerance by enhancing enzymatic activities and hormonal balance (Hasanuzzaman et al. 2018).